Coccolithophores (calcareous nannoplankton) distribution in the surface waters of the western Cretan Straits (South Aegean Sea): productivity and relation with the circulation pattern*

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ABSTRACT: Living coccolithophores were collected in February 2008, in surface waters from seven stations over the western Cretan Straits (South Aegean Sea, Eastern Mediterranean). The coccolithophore distribution was quantitatively documented through Scanning Electron Microscopy in terms of density, diversity and community structure. In the study period, the most abundant species was *Emiliania huxleyi*, followed by *Rhabdosphaera clavigera* and *Syracosphaera pulchra*, while additional important component of the winter assemblages were *Helicosphaera carteri*, *Algirosphaera robusta* and *Syracosphaera molischii*. The studied coccolithophore communities indicate a close relationship between coccosphere densities and surface water circulation, with the surface temperature gradient affecting species composition.
Key-words: *living coccolithophores*, *spatial distribution*, *Cretan Sea*.

ΠΕΡΙΛΗΨΗ: Η δειγματοληψία των σύγχρονων κοκκολιθοφόρων πραγματοποιήθηκε το Φεβρουάριο του 2008, σε επτά καθορισμένους σταθμούς στην περιοχή των δυτικών στενών της Κρητικής λεκάνης (Νότιο Αιγαίο πέλαγος, Ανατολική Μεσόγειος). Για τη μελέτη της κατανομής των κοκκολιθοφόρων εξετάστηκαν οι παράμετροι της περιεκτικότητας, της ποικιλότητας, της αφθονίας στη δομή της βιοκοινωνίας των κοκκολιθοφόρων. Κατά την περίοδο μελέτης, το είδος *Emiliania huxleyi* επικρατεί στις συγκεντρώσεις, ακολουθούν σε αφθονία τα είδη *Rhabdosphaera clavigera* και *Syracosphaera pulchra*, ενώ σημαντική συμμετοχή στις συναθροίσεις παρουσιάζουν τα είδη *Helicosphaera carteri*, *Algirosphaera robusta* και *Syracosphaera molischii*. Η μελέτη της βιοκοινωνίας κατέδειξε ότι, η κυκλοφορία των επιφανειακών υδάτινων μαζών επιδρά στις περιεκτικότητες των κοκκολιθοφόρων, ενώ η σύνθεση των ειδών επηρεάζεται από τη διακύμανση των επιφανειακών θαλάσσιων θερμοκρασιών.
Λέξεις-κλειδιά: *σύγχρονα κοκκολιθόφορα, οριζόντια χωρική κατανομή, Κρητική λεκάνη*.

INTRODUCTION

Coccolithophores constitute a significant component of the marine phytoplankton in modern oceans and are very sensitive to the changing environmental conditions of the upper water column. In particular, through photosynthesis and calcification they play an important role in the biogeochemical cycles and the global climate system (Westbroek *et al.*, 1993; Haidar & Theirstein, 2001; Rost & Riebesell, 2004).

Coccolithophores have a world-wide distribution in the oceans' photic zone, but prefer warm, low productivity regions (McIntyre & Be, 1967; Honjo & Okada, 1974; Cortés *et al.*, 2001). Therefore, they are among the dominant primary producers in the oligotrophic eastern Mediterranean Sea. The living coccolithophores in the Mediterranean Sea waters present a high number of species (e.g. Knapperstbusch, 1990; Kleijne, 1991, 1992, 1993; Ziveri *et al.*, 2000; Cros *et al.*, 2000; Cros & Fortuño, 2002; Saugestad & Heimdal, 2002; Triantaphyllou *et al.*, 2002; 2004a; 2004b; Triantaphyllou & Dimiza, 2003; Malinverno *et al.*, 2003, 2009; Balestra *et al.*, 2008; Dimiza *et al.*, 2008) with a strong seasonal variability and regional patchiness. In a trans-Mediterranean study conducted in June 1999, coccolithophores were more abundant and diversified at the eastern stations than at the western ones (Ignatiades *et al.*, 2009). The widespread species *Emiliania huxleyi* is generally the most frequent and dominant within this group. The oligotrophic character of the Mediterranean Sea, as well as the high seasonality in sea surface temperatures, solar radiation, nutrient concentrations and in the circulation of surface water masses affect the assemblage composition, diversity and productivity of living coccolithophores. Therefore, it is important to understand the response of coccolithophores to different oceanographic settings within the Mediterranean marine ecosystem.

The main objective of this study is to determine the cell density and species composition of modern coccolithophore communities in surface waters over the western Cretan Straits (South Aegean Sea, Eastern Mediterranean) during late winter 2008. Diversity indices (species richness, Shannon-Wiener and Dominance) and graphical examination of the contour maps of total standing crop and abundances of the most common coccolithophore species were used in order to

* Κατανομή των κοκκολιθοφόρων (ασβεστολιθικό ναννοπλαγκτόν) στα επιφανειακά ύδατα της περιοχής των δυτικών στενών της Κρητικής λεκάνης (Νότιο Αιγαίο πέλαγος): συσχετισμός της παραγωγικότητας με την κυκλοφορία των επιφανειακών υδάτινων μαζών

interpret the spatial distribution pattern and to infer the ecology of living communities.

ENVIRONMENTAL SETTING

The Cretan Sea is an active area, which plays a significant role in the circulation of the Eastern Mediterranean. It is not only the southernmost basin of the Aegean Sea but the largest in volume and the deepest one (Theocharis *et al*., 1999; Georgopoulos *et al*., 2000; Velaoras & Lascaratos, 2005), representing a reservoir for heat, salt and dissolved oxygen for the Eastern Mediterranean (Georgopoulos *et al*., 1989). It communicates with the Levantine Basin and the Ionian Sea through the eastern and the western Cretan Straits, respectively. The western Cretan Straits consist of Antikithira, Kithira and Elaphonissos straits which play an important role in the control of the exchanges of water and material (dissolved, suspended or near-bed) between the Aegean and the Ionian seas (Fig. 1).

The hydrological structure in the region is dominated by a complex and highly variable circulation pattern (Fig. 1), because of the interactions between the Myrtoan West Cretan cyclone, the West Cretan anticyclone and the anticyclonic Pelops Gyre (Theocharis *et al*., 1999), which are considered to control particle distribution and transfer in the area (Karageorgis *et al*., 2008). The water column is characterised by a persistent thermocline that induces strong stratification during most of the year and by intense mixing during the winter period.

Surface water circulation is dominated by low-salinity Modified Atlantic Waters (MAW), which intrudes into the Cretan Sea mainly through the Antikithira Strait and occasionally via the Kassos Strait, as well as by Black Sea origin Waters (BSW) which are occasionally detectable down to the Kitherian Straits (Theocharis *et al*., 1999). In the intermediate layers, a distinctive "nutrient rich-oxygen poor" layer with minimum salinity is formed by the intrusion of the Transitional Mediterranean Water (TMW), coming from mid-depths of the eastern Mediterranean through the Kassos and the Antikithira straits (Balopoulos *et al*., 1999; Lykousis *et al*., 2002) compensating for the massive Cretan Deep Water (CDW) outflow (Souvermezoglou *et al*., 1999). However the physicochemical characteristics of TMW have changed with time and an overall decrease of the volume and transport of CDW has been observed (Kontoyiannis *et al*., 2005).

The southern Aegean Sea waters are typically oligotrophic (Lykousis *et al*., 2002), poorer in nutrients and richer in oxygen than the adjacent Ionian and Levantine seas (Souvermezoglou *et al*., 1999). The observed oligotrophy in the area, in terms of both primary productivity and chlorophyll-a concentrations, is related to an eastward increase of phosphorus limitation resulting in an increase of the N/P ratio (Krom *et al*., 1991, 1992; Tselepides *et al*., 2000). The phytoplankton population of the modern eastern Mediterranean is dominated by flagellates including coccolithophores (Kleijne, 1991; Knappertsbusch, 1993; Ziveri *et al*., 2000; Malinverno *et al*., 2003; Triantaphyllou *et al*., 2004; Ignatiades *et al*., 2009).

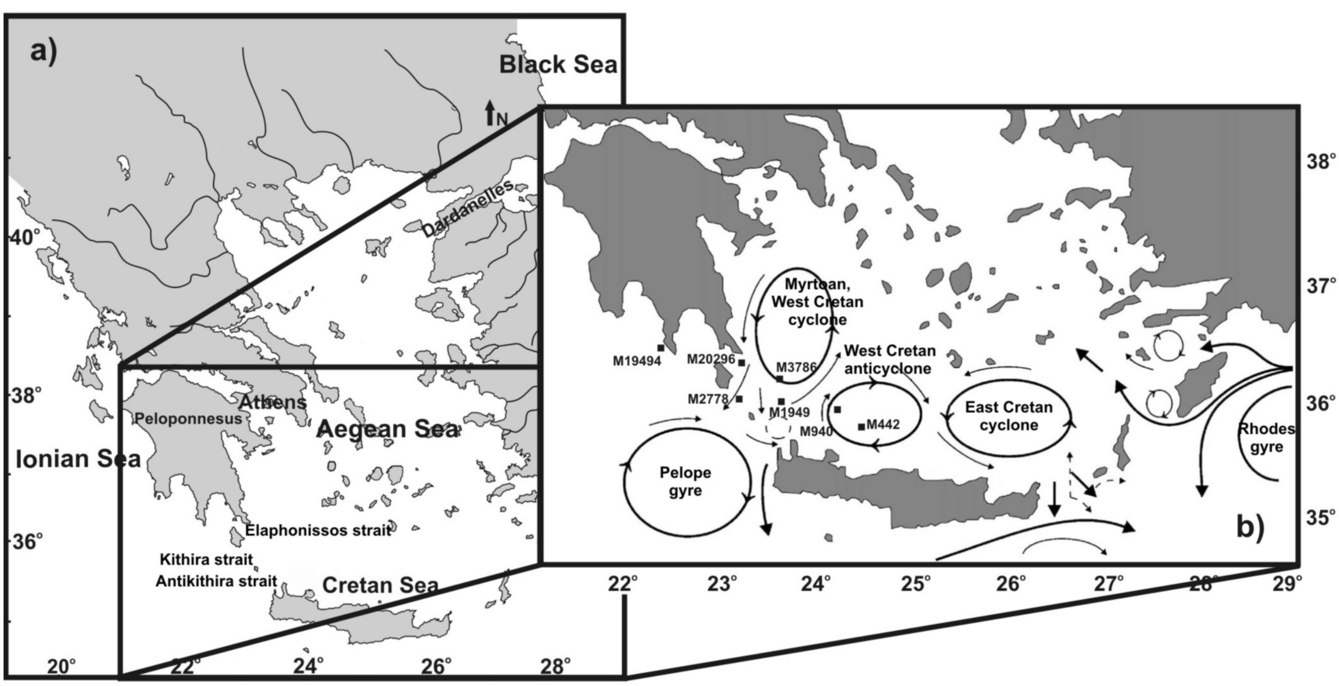

Fig. 1a. Map of the study area and b. location of the stations sampled for coccolithophore analysis with the main circulation features (according Theocharis *et al*., 1999).

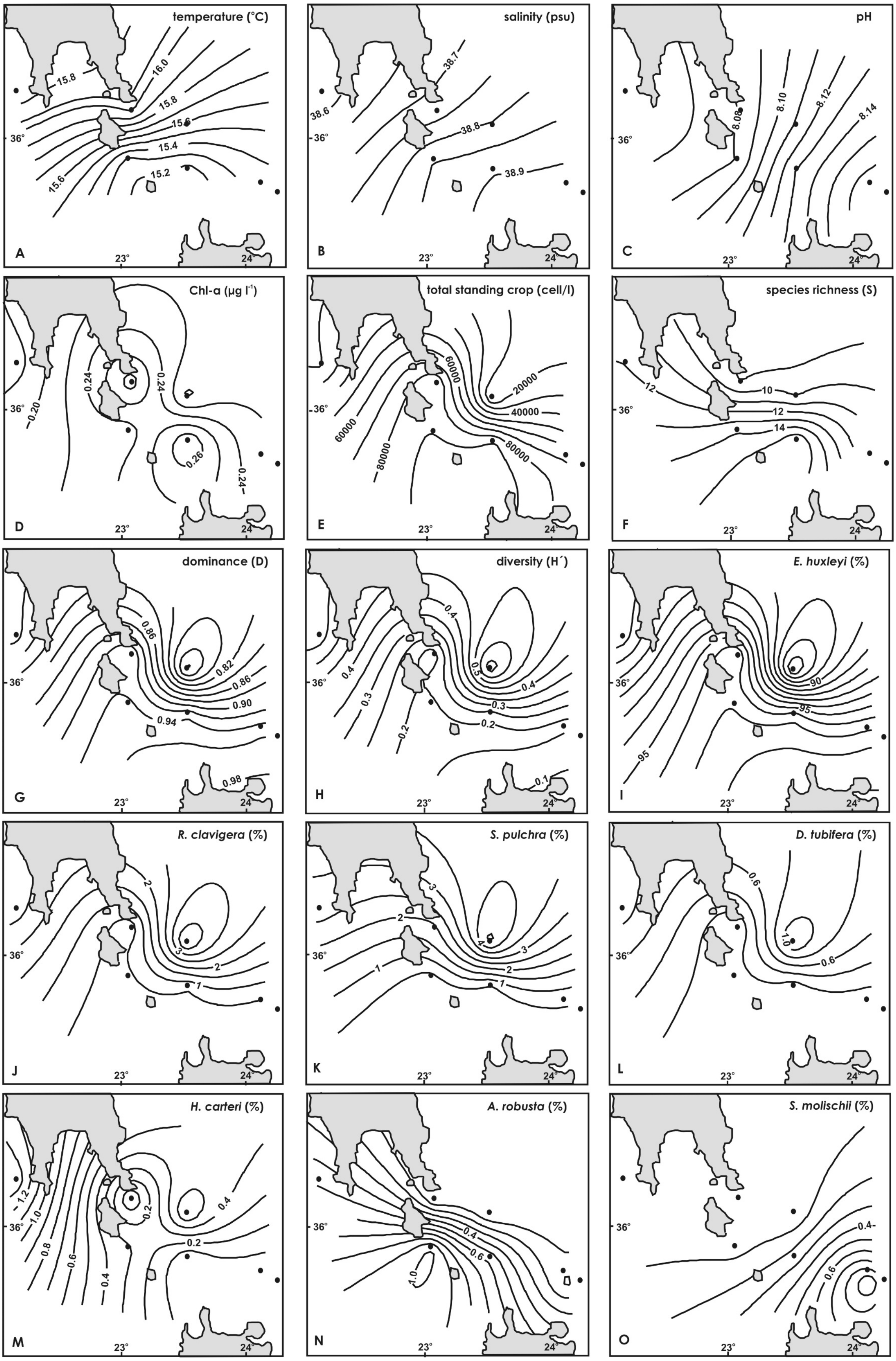

Fig. 2. Contour maps of environmental parameters (A-D), total standing crop (E), diversity indices (F-H) and abundances of the most common species (I-O).

TABLE 1
Location of stations, sampling dates, coccolithophore absolute abundances (cells/l), chlorophyll-a, pH, water temperature and salinity data.

Station	Date	Latitude	Longitude	Depth (m)	Coccolithophores (cells/l)	T (°C)	pH	S (‰)	Chl-a (mg m^{-3})
M442	27/2/2008	35°51,68΄N	24°28,83΄E	3	37860	15,36		38,92	0,220
M940	27/2/2008	35°54,73΄N	24°11,71΄E	3	73120	15,34	8,17	38,93	0,220
M1949	27/2/2008	36°00,44΄N	23°36,44΄E	3	91732	15,15	8,13	38,90	0,300
M2778	27/2/2008	36°04,54΄N	23°07,04΄E	3	90229	15,25	8,08	38,85	0,230
M3786	27/2/2008	36°18,30΄N	22°35,37΄E	3	9826	15,57	8,11	38,70	0,195
M19494	29/2/2008	36°29,78΄N	22°12,27΄E	3	18728	16,22	8,06	38,56	0,170
M20296	29/2/2008	36°22,78΄N	23°08,40΄E	3	89594	16,02	8,08	38,73	0,290

MATERIAL AND METHODS

Water samples for coccolithophore analysis were collected on 27-29 February 2008 in surface waters from seven stations (Fig. 1, Table 1) over the western Cretan Straits (South Aegean Sea, Eastern Mediterranean). Relevant temperature, salinity, pH and chlorophyll data are presented in Table 1. For each sampling station, 2 liters of seawater were filtered on Whatman cellulose nitrate filters (47mm diameter, 0.45μm pore size), using a vacuum filtration system. Salt was removed by washing the filters with about 2 ml of mineral water. The filters were open dried and stored in plastic Petri dishes. A piece of each filter approximately 8x8 mm^2 was attached to a copper electron microscope stub using a double-sided adhesive tape and coated with gold. The filters were examined in a Jeol JSM 6360 Scanning Electron Microscope (University of Athens, Department of Historical Geology and Paleontology) and all the individual coccospheres occurring on the examined filter area were identified and counted. A working magnification of 1200x was used throughout the counting. The absolute abundances of coccolithophore densities (number of coccospheres/liter) was calculated following the methodology of Jordan & Winter (2000), by scaling up the raw counts from a known scanned area, using the equation: A=NxS/V, where N is the number of coccospheres of a species on the whole piece of filter, S the scaling factor (area of the whole filter/area of scanned filter piece), V the volume of the sea water filtered (l) and A the absolute abundance of the species in coccospheres/l.

Diversity indices were calculated using the Past.exe 1.23 software package (Hammer *et al*., 2001), including species richness (S), Dominance (D) and Shannon–Wiener diversity index (H΄). Spatial distribution of environmental parameters, total standing crop, diversity indices and abundances of the most common species have been visualised by constructing contour maps in Surfer (version 8.0) using inverse distance to power gridding method (triangulation with linear interpolation).

RESULTS

Hydrography

The surface water along the transect showed a sea surface temperature interval from 15.15 °C to 16.22 °C and a salinity interval from 38.56 psu to 38.93 psu (Table 1). The average pH was near 8.10 and the average chlorophyll-a concentration was 0.23 μg l^{-1}.

The spatial distribution of the environmental parameters is presented in Figs 2A-D. Temperature increased towards the North, where the highest surface value (16.22 °C; Table 1) was found at the NW edge of the study area (Stn M19494) close to the Peloponnesus coasts. Surface salinity showed an opposite pattern with the lowest values occurring in the southeastern part of the sampling area. The pH values increased towards the East, while chlorophyll-a concentrations were quite variable (0.17–0.30), with a slight increase in the Kithira Strait area.

Coccolithophore community structure and species composition

The total coccosphere density in the study area varied between 9.8-91.7x10^3 cells/l (Stn M3786 and M1949, respectively) (Table 1). The highest densities were displayed at stations M20296, M2778, M1949 and M940, which are probably found at the periphery of the Myrtoan cyclone, whereas the lowest values were recovered at Stn M3786, likely corresponding to the central part of the gyre.

The coccolithophore community consisted of 26 heterococcolithophore and 4 holococcolithophore species. Overall, the highest species richness (16 taxa) was observed at Stn M1949 and the lowest (9 taxa) at Stn M20296. In Fig. 2F, species richness gradually increased towards the south, keeping pace with the temperature decline.

Coccosphere densities of species recorded in the study area are presented in Table 2. *Emiliania huxleyi* was the dominant species always accounting for more than 85% of the assemblage (Fig. 2I). Other important taxa like the Rhabdosphaeraceae (mainly *Rhabdosphaera clavigera*, *Discosphaera tubifera* and *Algirosphaera robusta*) and different species of *Syracosphaera* (mostly *S. pulchra* and *S. molischii*) were scarce at all stations, with relative abundance values lower than 10%. *R. clavigera* and *S. pulchra* were umbiquitous and exhibited more or less similar distribution patterns as *Discosphaera tubifera* (Figs 4J-L), with maximum abundance in the northern part of the sampling area.

The distribution pattern of *Helicosphaera carteri* (Fig. 4M) was somewhat different, with a tendency to higher values in the western part of the sampling area. In contrast, *A. robusta* and *S. molischii* (Figs 4N-O) gradually increased in abundance towards the South, along with the increase in *E. huxleyi* coccosphere density. Finally, other species such as *Umbilicosphaera sibogae, Calcidiscus quadriperforatus* and *Coronosphaera mediterranea* also occurred throughout the sampling area (Table 2), but were generally less than 1 % of the total assemblages.

The dominance index values ranged from 0.75 (Stn M3786) to 0.96 (Stns M940 and M442), while low Shannon diversity values (max=0.63 at Stn M3786) were documented. Contour maps, in Figs 2G-H, display the spatial distribution of diversity indices. The highest values of the dominance index are followed by low Shannon diversity and coincide with increasing cell densities.

DISCUSSION

The winter coccolithophore assemblages in the vicinity of the western Cretan Straits (South Aegean Sea, Eastern Mediterranean) are characterized by high coccosphere densities and high dominance values (associated with low values of Shannon diversity). These features indicate rather eutrophic conditions (Margalef, 1978). In late winter, the convective mixing processes are intensified, resulting in the replenishment of the euphotic zone with nutrients transferred from deeper waters (Tselepides *et al*., 2000). The doming of isopycnals within the Myrtoan West Cretan cyclone has possibly increased the vertical transport of nutrients at the time of the winter convective event and has created favorable conditions for primary production. The availability of nutrients can be very important for the increase in abundance of opportunistic (r-selected) species, such as *E. huxleyi*, a species well known for its quick response to nutrient enrichment

TABLE 2
Coccolithophore species (cells/l) recorded at western Cretan Straits during February 2008 sampling.

station	M442	M940	M1949	M2778	M3786	M19494	M20296
coccolithophores (cells/l)							
Acanthoica quattrospina	60	0	230	60	0	0	0
Algirosphaera robusta	120	60	520	920	0	90	0
Alisphaera unicornis	0	60	0	0	0	0	70
Anacanthoica acanthos	0	60	0	0	0	0	0
Calcidiscus quadriperforatus	60	60	0	120	60	0	140
Calciosolenia brasiliensis	0	0	0	60	0	90	70
Coronosphaera mediterranea	60	0	60	290	0	0	360
Cyrtosphaera lecaliae	0	0	60	0	0	0	0
Discosphaera tubifera	0	0	60	120	120	170	0
Emiliania huxleyi	37050	71430	88610	87500	8500	16470	86990
Helicosphaera carteri	0	0	0	290	60	260	0
Helicosphaera hyalina	0	0	0	0	60	0	0
Helicosphaera wallichii	0	60	0	0	0	90	0
Pontosphaera syracusana	0	0	0	0	120	0	0
Rhabdosphaera clavigera	120	120	520	350	400	520	140
Scyphosphaera apsteinii	0	0	0	60	0	0	0
Syracosphaera ampliora	60	60	60	0	0	0	0
Syracosphaera anthos	60	0	0	0	0	0	0
Syracosphaera histrica	0	0	170	0	60	0	70
Syracosphaera molischii	120	740	230	60	0	0	70
Syracosphaera nodosa	0	60	0	60	0	0	0
Syracosphaera pulchra	60	290	350	290	460	520	1660
S. sp. aff. S. *orbiculus*	60	0	0	0	0	0	0
Umbellosphaera tenuis type II	0	0	60	0	0	170	0
Umbilicosphaera foliosa	0	0	60	0	0	90	0
Umbilicosphaera sibogae	60	120	400	0	60	90	0
Holococcolithophores (cells/l)	0	0	230	60	0	90	0
Anthosphaera periperforata	0	0	0	60	0	0	0
Helladosphaera cornifera	0	0	60	0	0	0	0
Syracolithus dalmaticus	0	0	170	0	0	0	0
S. pulchra HOL *pirus* type	0	0	0	0	0	90	0

(e.g., Hulburt, 1982, 1985; Broerse *et al*., 2000; Tyrrell & Merico, 2004). Our results confirm the findings of Malinverno *et al*. (2009), who studied, through sediment trap deployments, the seasonal and spatial variability of coccolithophore export production at the South-Western margin of Crete from 2005 to 2006. They showed that *E. huxleyi* prevails in the period of maximum coccosphere export during the water column mixing phase, which also coincides with the interval of increased rainfall in the late winter–spring.

In the present study, a close relationship between the distribution of the coccolithophore species and the pattern of surface water circulation was detected. A general increase in total coccosphere density is observed, following the direction of surface water masses that move towards the Kitherian Straits. Although we lack a comprehensive dataset on the size, position and strength of the mesoscale circulation features during the present study, our findings imply the influence of the Myrtoan West Cretan Gyre on the coccolithophore assemblages. The abundance and distribution of marine phytoplankton is primarily controlled by factors affecting their growth (nutrient availability, radiant energy) and dispersal (water stability, currents). The violent vertical mixing in correspondence to the Myrtoan cyclone causes the upwelling of nutrient-rich deep waters which subsequently flow horizontally at the surface towards the outer margin of the gyre. This nutrient supply most probably promoted the growth of phytoplankton and its accumulation in the upper layer at the periphery of the cyclonic structure. Oceanographic surveys made during the ’90s have shown that the southern edge of the Myrtoan West Cretan cyclone reaches the western Cretan straits (Theocharis *et al*., 1999; Kontoyiannis *et al*., 2005). Relatively lower chlorophyll-a concentration and total cell density are apparently recorded in the center of the Myrtoan West Cretan Gyre (Stn M3786). It

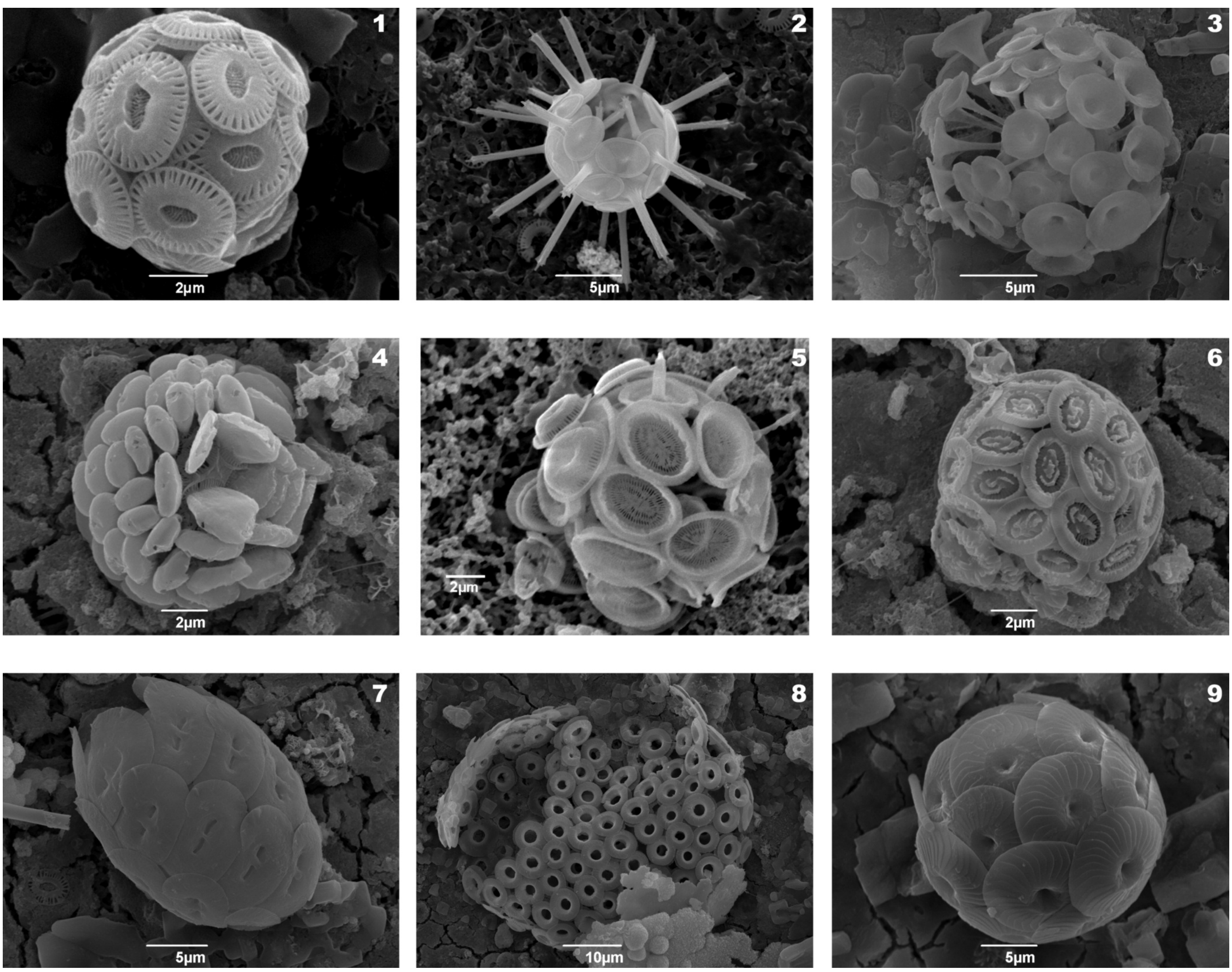

PLATE I

1. *Emiliania huxleyi*, station 940, **2.** *Rhabdosphaera clavigera*, station 940, **3.** *Discosphaera tubifera*, station 2278, **4.** *Algirosphaera robusta*, station 2278, **5.** *Syracosphaera pulchra*, station 20296, **6.** *Syracosphaera molischii*, station 2278, **7.** *Helicosphaera carteri*, station 2278, **8.** *Umbilicoshaera sibogae*, station 1949, **9.** *Calcidiscus quadriperforatus*, station 20296.

seems that the strong convective mixing in the core of the Gyre establishes an unstable and extremely dynamic environment that disorganizes the phytoplanktonic communities and highly limits the build-up and accumulation of phytoplanktonic biomass.

In the area close to the southeastern Peloponnesus coasts that is characterized by slightly higher temperature, coccolithophore concentrations displayed the lowest values. The high values of Shannon index reflect a considerable increase of species concentration. Therefore, although the assemblages are still dominated by *E. huxleyi*, other important taxa such as *R. clavigera*, *S. pulchra* and *D. tubifera* are relatively well represented there. These species are less opportunistic and are considered as indicative of intermediate environments with intermediate nutrient conditions (Young, 1994; Triantaphyllou *et al*., 2002; Dimiza *et al*., 2008). In the waters of the Eastern Mediterranean, they are commonly concentrated during the warm season (Knappertsbusch, 1993; Ziveri *et al*., 2000; Triantaphyllou *et al*., 2002, 2004b; Malinverno *et al*., 2003; Balestra *et al*., 2008; Dimiza *et al*., 2008). Another species that is known for its preference for warm waters (McIntyre & Bé, 1967; Gard & Backman, 1990; Brand, 1994; Baumann *et al*., 2005), but moderately elevated nutrient conditions (Ziveri *et al*., 1995; Ziveri *et al*., 2000; Findlay & Giraudeau, 2000; Andruleit & Rogalla, 2002; Ziveri *et al*., 2004) is *H. carteri*. In the present dataset, this species is slightly more abundant in the western area.

In contrast, the communities showing the higher densities are located near the northwestern coasts of Crete, where temperatures are ~1°C lower. In these communities, the high species richness is coupled with low diversity and high dominance: this implies that the higher number of species in these samples represents only a small part of the assemblages while *E. huxleyi* contributes the largest portion of the high coccosphere counts. According to the species distribution, the presence of *S. molischii* and *A. robusta* is associated with higher abundances of *E. huxleyi*. *S. molischii* is well known for its preference for relatively eutrophic environments (Giraudeau, 1992; Andruleit & Rogalla, 2002; Dimiza *et al*., 2008), while *A. robusta* displays a flexible response to nutrient availability, even at shallow depths (Jordan & Winter, 2000; Andruleit & Rogalla, 2002; Malinverno *et al*., 2003, 2009).

CONCLUSIONS

Total coccolithophore densities in the marine ecosystems of the western Cretan Straits (North Aegean Sea) during late winter 2008 varied between 9.8×10^3 and 91.7×10^3 coccospheres/l. In total, 30 different coccolithophore species are recognized, of which *E. huxleyi* represents more than 85 %. The present study shows that coccolithophore communities are affected by surface water circulation, and their peak concentration occurred at the outer margin of the Myrtoan cyclone in the proximity of the Kitherian Straits. In most samples, the coccolithophore community is characterized by high total standing crop and dominance values, whereas Shannon diversity is low. However, the Shannon–Wiener index rises gradually in the area close to the southeastern Peloponnesus coasts, due to the increase of less opportunistic species such as *R. clavigera*, *S. pulchra* and *D. tubifera* that suggests a trend to warmer and intermediate environments with normal nutrient conditions. In contrast, the dominance index exhibits an opposite pattern, following the increase in *E. huxleyi* and the occurrence of other eutrophic species such as *A. robusta* and *S. molischii*.

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